

# Covert manual response preparation triggers attentional modulations of visual but not auditory processing

Martin Eimer <sup>\*</sup>, José van Velzen

*School of Psychology, Birkbeck College, University of London, UK*

Accepted 11 January 2006

Available online 3 March 2006

---

## Abstract

**Objective:** We investigated whether covert unimanual response preparation triggers attention shifts, as postulated by the premotor theory of attention, and whether these result in spatially specific modulations of visual and auditory processing.

**Methods:** Visual response cues instructed participants to prepare to lift their left or right index finger in response to a subsequent target stimulus. Irrelevant visual or auditory probes were delivered to the left or right hand during the response preparation interval. ERPs were measured time-locked to cue onset, and time-locked to probe stimulus onset.

**Results:** Lateralised ERP components triggered during covert response preparation (ADAN, LDAP) were similar to components previously found during attention shifts. N1 components were enhanced to visual probes delivered adjacent to the cued response relative to those delivered to the opposite hand. Auditory probe ERPs were unaffected by manual response preparation.

**Conclusions:** Shifts of spatial attention that are triggered during covert unimanual response preparation result in spatially specific modulations of visual but not auditory processing.

**Significance:** Results support the claim of the premotor theory that the preparation of manual responses is associated with attention shifts. However, such shifts are not based on purely supramodal processes, as they result in a modality-specific pattern of sensory modulations.

© 2006 International Federation of Clinical Neurophysiology. Published by Elsevier Ireland Ltd. All rights reserved.

**Keywords:** Attention; Spatial; Response preparation; Event-related brain potentials; Visual processing; Auditory processing

---

## 1. Introduction

Numerous studies have investigated the mechanisms responsible for the control of covert shifts of spatial attention, and the effects that such attentional shifts have on the processing of stimuli at currently attended versus unattended locations. These issues are traditionally studied independently for different sensory modalities, with little contact between researchers interested in attentional control processes in vision, audition, or touch. The question whether there might be crossmodal links in spatial attention has only begun to be addressed systematically in the last decade (see Driver and Spence, 1998, for review).

Recent studies have uncovered the existence of strong spatial synergies in selective attention across sensory modalities. When attention is directed to the expected location of task-relevant events within one (primary) stimulus modality, performance benefits can also be observed for target stimuli of another (secondary) modality at this location, even though these stimuli are just as likely to be presented at other locations (e.g. Spence and Driver, 1996; Spence et al., 2000; see also Butter et al., 1989; Ward, 1994, for related findings). These behavioural findings have been complemented by ERP results demonstrating that when attention is directed to a specific location for a task within one primary modality (vision, audition, or touch), early, sensory-specific ERP components triggered by stimuli in another, entirely irrelevant stimulus modality are enhanced when these stimuli are presented at

---

\* Corresponding author.

E-mail address: m.eimer@bbk.ac.uk (M. Eimer).

the attended location (e.g. Eimer and Driver, 2000; Eimer and Schröger, 1998; Hillyard et al., 1984; Teder-Sälejärvi et al., 1999).

While these behavioural and electrophysiological findings demonstrate the existence of crossmodal links in spatial attention between vision, audition and touch, they are consistent with different hypotheses about the nature of the underlying mechanisms. These crossmodal interactions might reflect a supramodal control system for spatial attention, which directs attention to task-relevant locations irrespective of the sensory modality of anticipated sensory events (Farah et al., 1989). Alternatively, the presence of crossmodal links in attention is equally consistent with horizontal links between otherwise separate, modality-specific attentional control systems (as suggested by Spence and Driver, 1996).

A way to distinguish between these possibilities is to directly measure electrophysiological correlates of attentional control processes during the time interval when covert shifts of attention take place. A number of studies have analysed ERPs obtained in the interval between cue stimuli directing visual attention to the left or right side and the onset of a subsequent lateral imperative stimulus. To identify ERP components sensitive to the direction of cued attentional shifts, these studies have compared ERP waveforms triggered in response to cues directing attention to the left side to ERPs elicited during rightward attentional shifts (c.f. Harter et al., 1989; Hopf and Mangun, 2000; Nobre et al., 2000; Yamaguchi et al., 1994). At anterior recording sites, ERPs were more negative over the hemisphere contralateral to the cued attentional shift relative to ERPs elicited ipsilaterally ('Anterior Directing Attention Negativity', ADAN). This effect had an onset latency of about 350 ms after cue onset, and was followed at about 500 ms post-stimulus by an enhanced posterior positivity over the contralateral hemisphere ('Late Directing Attention Positivity', LDAP). These lateralised ERP components were interpreted as reflecting successive phases in the control of visual-spatial orienting, such as the initiation of an attention shift and the preparatory activation of sensory-specific cortical areas<sup>1</sup>.

Because ERP studies of attentional orienting cited above only investigated spatial shifts of visual attention, they did not address the question whether attentional shifts are controlled by modality-specific or supramodal processes. However, some recent experiments have directly compared

ERPs elicited during attentional shifts in the context of visual, auditory, and tactile tasks (Eimer et al., 2002, 2003; Eimer and Van Velzen, 2002; Van Velzen et al., 2002). Intriguingly, very similar ADAN and LDAP components were found during shifts of attention towards task-relevant tactile, visual, or auditory events, suggesting that these components may reflect the activity of a single supramodal attentional control system (see Eimer et al., 2002; Eimer and Driver, 2001; for more detailed discussion).

In addition to such experimental data suggesting the existence of supramodal attentional networks, the assumption that shifts of attention are mediated by modality-unspecific control structures is also implied by the premotor theory of attention. According to this theory, the control of goal-directed movements and the control of attention are both implemented by common mechanisms. Shifts of attention are triggered whenever these shared control structures are activated during response preparation (Rizzolatti et al., 1994). There may be important anatomical and functional dissociations between different attentional-motor control mechanisms specialised for different types of movements and for different parts of space. However, and importantly, these mechanisms are unlikely to be completely modality-specific, as their function is to select and utilise information from different sensory channels whenever this information is relevant for the control of response selection and execution. Thus, the premotor theory may offer a natural and parsimonious explanation for the existence of crossmodal spatial links in attention by regarding such links as a natural consequence of the fact that attention and motor processes are implemented by common control structures.

The most compelling evidence supporting the premotor theory of attention comes from studies demonstrating links between shifts of attention and eye movement preparation. The fact that overlapping frontoparietal control structures are activated during the covert orienting of visual attention and during saccade preparation (Corbetta et al., 1998) suggests that the programming of saccadic eye movements and shifts of visual attention are based on common mechanisms. Additional behavioural evidence for this hypothesis comes from studies demonstrating that attention shifts towards saccade target locations are triggered during saccade preparation (Hoffman and Subramaniam, 1995; Irwin and Gordon, 1998), and that these attention shifts affect performance even before the eyes have begun to move (Deubel and Schneider, 1996). Furthermore, the trajectory of eye movements is affected by the current focus of visual attention (Sheliga et al., 1995), even for saccades triggered via stimulation of the superior colliculus (Kustov and Robinson, 1996). There is now also some initial evidence that eye movement preparation has similar spatially selective attentional effects on the processing of auditory (Rorden and Driver, 1999) and tactile stimuli (Rorden et al., 2002), which is consistent with the hypothesis that

<sup>1</sup> An early contralateral negativity over posterior sites that was reported in several ERP studies ('Early direction attention negativity', EDAN) is likely to reflect the processing of non-symmetrical (i.e. arrow) cues, rather than processes directly involved in the control of anticipatory attentional shifts (see Van Velzen and Eimer, 2003, for evidence). To avoid ERP lateralisations caused by asymmetrical cues, and to minimize the possibility that such cue stimuli would result in automatic shifts of attention (see Tipples, 2002, for behavioural evidence that non-symmetrical arrow cues can automatically trigger attentional orienting), a cueing procedure with symmetrical arrow cues was used in the present study.

the attentional-motor control structures involved are modality-unspecific.

Importantly, the premotor theory of attention explicitly assumes that links between attention and response preparation are not restricted to oculomotor control, but should also be present for other types of actions, such as unimanual responses (Rizzolatti et al., 1994). Because there is as yet very little evidence for such links outside the oculomotor domain, we have recently used ERP measures to investigate whether shifts of attention are triggered when unimanual responses are covertly prepared (Eimer et al., 2005). ERPs were recorded while participants were covertly preparing to lift their left or the right index finger (as indicated by visual cues presented at the start of each trial). The cued response had to be executed (or withheld) after the presentation of a visual Go (or Nogo) signal. ERP waveforms recorded during covert response preparation in response to cues signaling an upcoming left-hand response were compared to ERPs following cues that signaled a right-hand response (see also Wauschkuhn et al., 1997; Verleger et al., 2000; Van der Lubbe et al., 2000, for similar procedures to measure ERP correlates of response preparation). Intriguingly, this comparison revealed lateralised ERP modulations that were very similar to the effects previously observed during cued attentional shifts towards task-relevant visual, auditory, or tactile events. A negativity at anterior electrodes contralateral to the side of the cued response was followed by an enhanced positivity over contralateral posterior electrodes.

This similarity between lateralised ERP components elicited during explicitly cued shifts of spatial attention and during cued unimanual response preparation suggests that the preparation of hand movements gives rise to attentional shifts, as predicted by the premotor theory of attention. To further investigate whether such attention shifts triggered during manual response preparation also affect sensory stimulus processing, we also included task-irrelevant tactile probe stimuli that were delivered during the covert response preparation interval to the left or right hand (see Eimer et al., 2005, for details). Early somatosensory ERP components (P90, N140) were enhanced for tactile probes delivered to the cued versus uncued hand, similar to attentional modulations of somatosensory ERP components previously observed as a result of explicitly instructed covert shifts of tactile attention (Michie et al., 1987; Eimer and Forster, 2003a, 2003b).

The aim of the present experiment is to obtain further ERP evidence that manual response preparation gives rise to spatially specific modulations of sensory stimulus processing. While our previous study (Eimer et al., 2005) demonstrated response hand preparation effects on somatosensory processing, we now investigated the possibility that shifts of spatial attention elicited during manual response preparation would also result in modulations of visual and auditory processing. The presence of such effects would provide new support for the view that modality-unspecific

attentional-motor control mechanisms are activated during the preparation of left-hand and right-hand responses.

The overall procedure used was similar to our previous experiment (Eimer et al., 2005), except that tactile probe stimuli were now replaced by visual or auditory probes. A visual response cue presented centrally at the start of each trial instructed participants to prepare to lift their left or right index finger. 1100 ms after the onset of this response cue, a visual Go or Nogo stimulus (the letters 'G' or 'S') appeared at fixation, prompting participants to either execute or to withhold the cued response. Go signals appeared on 80% of all trials, and Nogo signals were presented on the remaining 20%. This task required participants to monitor task-relevant visual events at fixation in order to select a response hand and to discriminate Go and Nogo stimuli. This was done to ensure that participants had no incentive to voluntarily move visual attention away from fixation towards the cued response side, or to prepare lateral eye movements during the response preparation interval. 900 ms after response cue onset (200 ms prior to the onset of the imperative visual Go/Nogo stimulus), a single task-irrelevant visual or auditory stimulus was presented with equal probability close to the cued or uncued hand. Participants were instructed to completely ignore these stimuli.

To investigate whether unimanual response preparation would result in shifts of spatial attention, and whether such attention shifts would affect the processing of visual and auditory stimuli, two sets of analyses were conducted. One set of analyses, which compared ERP waveforms triggered by response cues signaling an upcoming left-hand versus right-hand response, was expected to confirm our previous finding (Eimer et al., 2005) that lateralised ERP components known to be elicited during cued attentional shifts (ADAN, LDAP) are also triggered during unimanual response preparation. In addition, a contralateral negativity with a narrow focus over motor cortex was expected to emerge during later stages of the response preparation interval, reflecting the Lateralised Readiness Potential (LRP), which is an electrophysiological indicator of unimanual response activation (see Eimer, 1998; Eimer and Coles, 2003, for more details).

Most importantly, the second set of analyses was based on ERP waveforms triggered by task-irrelevant visual and auditory probe stimuli. Visual and auditory ERP waveforms elicited by these probes were compared as a function of whether probes were delivered close to the cued or uncued hand. If covert unimanual response preparation gives rise to attentional shifts that are modality-unspecific, as implied by the premotor theory of attention (see above), these attention shifts should result in systematic modulations of auditory and visual probe ERPs. More specifically, the effects of manual response preparation on visual and auditory ERPs should be similar to the effects of crossmodal spatial attention observed in earlier ERP studies for task-irrelevant visual and auditory events (e.g. Eimer and Schröger, 1998;

Hillyard et al., 1984; Teder-Sälejärvi et al., 1999), with larger sensory-specific visual and auditory ERP components for probe stimuli presented close to the cued response hand, as compared to probes delivered close to the opposite uncued hand. In contrast, the finding that attentional modulations of visual and auditory probe ERPs are entirely absent, or are only elicited for one sensory modality, would call into question the hypothesis that covert manual response preparation triggers modality-unspecific attention shifts.

## 2. Methods

### 2.1. Participants

Sixteen neurologically unimpaired subjects (9 females and 7 males; 21–35 years old; average age: 26.7 years) participated in this study. All subjects were right-handed and had normal or corrected-to-normal vision by self-report. The experiment was performed in compliance with relevant institutional guidelines, and was approved by the ethics committee of Birkbeck College, School of Psychology.

### 2.2. Stimuli and apparatus

Subjects were seated in a dimly lit sound attenuated cabin, viewing a computer screen placed at a distance of 70 cm. Hands were positioned on the left and right side, with index fingers located 25 cm to the left and right of the body midline. On each trial, a visual response cue (100 ms duration; indicating which hand was to be used in response to an upcoming visual Go signal) was followed by a visual imperative stimulus (Go or Nogo) that was presented 1100 ms after cue onset. Visual response cues consisted of two adjacent triangles, presented centrally on a computer screen (visual angle:  $3.5^\circ \times 2.5^\circ$ ). One triangle was red, the other blue, and they always pointed in opposite directions ('>' <' or '<' >'). A central fixation cross, located between both triangles, was present throughout the experimental blocks. Response side (left hand or right hand) for each trial was signalled by the direction of one of the triangles. For half of the participants, blue triangles were relevant, and red triangles were relevant for the other half. Relevant left-pointing or right-pointing triangles were presented with equal probability to the left or right of fixation. Uppercase letters 'G' (Go) and 'S' (Stop) served as Go and Nogo stimuli, respectively. They subtended a visual angle of  $0.8^\circ \times 0.9^\circ$  and were presented at fixation for 100 ms, where they replaced the fixation cross during this period.

In addition to visual response cues and Go–Nogo stimuli, each trial also contained one task-irrelevant auditory or visual event (probe), which was presented 900 ms after cue onset. Auditory probe stimuli were bursts of white noise

(100 ms duration; amplitude 80 dB SPL) presented from one of two loudspeakers located on the left and right side, adjacent to each hand. Visual probe stimuli were 100 ms illuminations of one of two ensembles of green LEDs that were positioned on the left and right side, adjacent to each hand. These LED ensembles consisted of 6 segments arranged in a circle plus one central segment. The angular size of each LED was  $0.65^\circ$ , the diameter of the circle was  $2.4^\circ$  and the mean luminance of each LED ensemble was approximately  $40 \text{ cd/m}^2$ .

### 2.3. Procedure

Twelve blocks of 80 trials each were conducted. Each trial started with the presentation of a response cue (100 ms duration). The imperative stimulus (Go or Nogo) was delivered 1100 ms after cue onset. Go stimuli were presented on 64 trials per block, while Nogo stimuli were delivered on the remaining 16 trials. On each trial, a visual or auditory probe stimulus was presented with equal probability 900 ms after cue onset (200 ms prior to imperative stimulus onset). These probe stimuli were presented with equal probability near the cued or uncued hand. Thus, every block contained eight Go trials and two Nogo trials for each combination of cued hand (left versus right), probe stimulus modality (visual versus auditory), and probe stimulus location (left versus right).

Participants were instructed to maintain central fixation, to ignore all visual or auditory probes, and to lift the index finger of the cued hand as fast as possible in response to the letter 'G', but to refrain from responding when the letter 'S' was presented. Manual response times were measured via an infrared response system consisting of a transmitter and receiver LED located on either side of the middle segment of the left and right index fingers in the resting position. A response was registered when an index finger was lifted, allowing the light beam of the transmitter LED to reach the receiver LED. On trials with incorrect responses (lifting of the uncued finger), or without any response, a visual feedback stimulus (the letter X) was presented 850 ms after Go stimulus onset for 50 ms at fixation, and these trials were excluded from analysis. The interval between the onset of a visual imperative stimulus on the preceding trial and the onset of the response cue on the subsequent trial was 2450 ms.

### 2.4. Recording and data analysis

EEG was recorded with Ag–AgCl electrodes and linked-earlobe reference from Fpz, F7, F3, Fz, F4, F8, FC5, FC6, T7, C3, Cz, C4, T8, CP5, CP6, P7, P3, Pz, P4, P8, and Oz (according to the 10–20 system), and from OL and OR (located halfway between O1 and P7, and O2 and P8, respectively). Horizontal EOG (HEOG) was recorded bipolarly from the outer canthi of both eyes. Electrode impedance was kept below  $5 \text{ k}\Omega$ , and the impedances of

the earlobe electrodes were kept as equal as possible. Amplifier bandpass was 0.1–40 Hz, and digitisation rate was 200 Hz. Trials with eyeblinks (voltage at Fpz exceeding  $\pm 80 \mu\text{V}$ ), horizontal eye movements (voltage at HEOG exceeding  $\pm 30 \mu\text{V}$ ), or muscle artefacts (voltage at any other electrode exceeding  $\pm 80 \mu\text{V}$ ) in the 1200 ms interval following response cue onset were excluded prior to data analysis.

Statistical analyses were conducted on the basis of ERP mean amplitudes obtained within predefined measurement windows during the covert response preparation interval. Separate analyses were run for ERPs following left and right response cues, and for ERPs triggered by visual and auditory probe stimuli. ERPs triggered by the visual response cues were averaged relative to a 100 ms baseline prior to the onset of these cues for the time interval between cue onset and 1200 ms after cue onset (100 ms after the onset of the subsequently presented imperative visual stimulus). Separate averages were computed for trials where cues indicated an upcoming left-hand or right-hand response (collapsed across Go and Nogo trials, and across trials with a visual or auditory probe on the left or right side). ERP mean amplitudes were analysed with repeated measures ANOVAs, and separate analyses were conducted for lateral anterior, central, and posterior sites. These analyses included the factors electrode site (F7/8 vs. F3/4 vs. FC5/6, for the anterior analysis, C3/4 vs. T7/8 vs. CP5/6, for the central analysis, and OL/R vs. P3/4 vs. P7/8, for the posterior analysis), cued response (left vs. right), and hemisphere (left vs. right). It is important to note that in these analyses, the presence of ERP lateralisations sensitive to the side of a cued response will be reflected by significant hemisphere  $\times$  cued response interactions. As in our earlier study (Eimer et al., 2005), analyses of ERPs following the response cues were based on mean amplitudes obtained within three successive post-cue latency windows between 350 and 600 ms (where the ADAN was previously observed), between 600 and 900 ms (where the LDAP component was found) and between 900 and 1200 ms (where an LRP was expected to emerge).

Next, averages were computed for ERPs triggered by visual and auditory probe stimuli. Probe ERPs were averaged relative to a 100 ms baseline prior to probe stimulus onset for the 300 ms interval after probe onset. Separate averages were computed for all combinations of probe modality (visual versus auditory), cued response (left vs. right) and stimulus location (left vs. right). Separate analyses were conducted for visual and auditory ERPs. For visual ERPs, mean amplitudes were computed within latency windows centred on the peak amplitudes of P1, N1, and P2 components (P1: 90–120 ms post-stimulus; N1: 160–200 ms post-stimulus; P2: 210–250 ms post-stimulus). For auditory ERPs, mean amplitudes were conducted within the N1 and P2 latency ranges (N1: 100–130 ms post-stimulus; P2: 180–220 ms post-stimulus). These mean amplitude values were analysed with repeated measures

ANOVAs, separately for midline electrodes (Fz, Cz, Pz), and for lateral anterior, central, and posterior sites. Analyses included the factors electrode site (F7/8 vs. F3/4 vs. FC5/6, for anterior electrodes, C3/4 vs. T7/8 vs. CP5/6, for central electrodes, OL/R vs. P3/4 vs. P7/8, for posterior electrodes, Fz vs. Cz vs. Pz, for midline electrodes), hemisphere (left vs. right, for lateral electrodes only), response preparation (probe presented close to cued vs. uncued hand), and probe stimulus side (left vs. right).

Manual response times (RTs) to Go stimuli were analysed in a repeated measures ANOVA for the factors response hand (left vs. right), probe stimulus modality (visual vs. auditory), and probe stimulus location (left vs. right). For all analyses, Green-house-Geisser adjustments to the degrees of freedom were applied where appropriate.

### 3. Results

#### 3.1. Behavioural performance

Manual RTs to Go stimuli were faster for right-hand than for left-hand responses (352 ms vs. 359 ms,  $F(1,15)=6.4$ ;  $P<.05$ ). In addition, RTs were slightly faster for trials with auditory probes than for trials with visual probes (351 ms vs. 359 ms,  $F(1,15)=5.5$ ;  $P<.05$ ). A response hand  $\times$  probe stimulus location interaction,  $F(1,15)=27.4$ ;  $P<.001$ , reflected the fact that RTs were faster when probes were presented to the cued hand (352 ms) relative to trials where probes were presented to the uncued hand (358 ms). This RT difference was larger for trials with visual probe stimuli (10 ms) than for trials with auditory stimuli (2 ms), as indicated by a three-way interaction (response hand  $\times$  probe stimulus location  $\times$  probe stimulus modality,  $F(1,15)=10.8$ ;  $P<.01$ ). False alarms occurred on 17.4% of all Nogo trials. Participants failed to respond on 1.2% of all Go trials, and responded prematurely on 0.25% of these trials. Incorrect responses (i.e. responses with the uncued hand) were virtually absent for all participants.

#### 3.2. ERPs elicited during covert response preparation

ERP modulations sensitive to the side of a cued unimanual response are shown in Fig. 1 for anterior (F7/8) and posterior (P7/8) electrode pairs in response to cues signalling that a left-hand or right-hand response was to be prepared. These waveforms show the 900 ms interval between response cue onset and the onset of a probe stimulus, and are collapsed across trials containing visual or auditory probes on the left or right side. They show early visual components (P1, N1) triggered by the response cue. As in our earlier study of lateralised ERP correlates of response preparation (Eimer et al., 2005), an enhanced anterior negativity contralateral to the side of the cued response (ADAN) was elicited about 350 after cue onset,

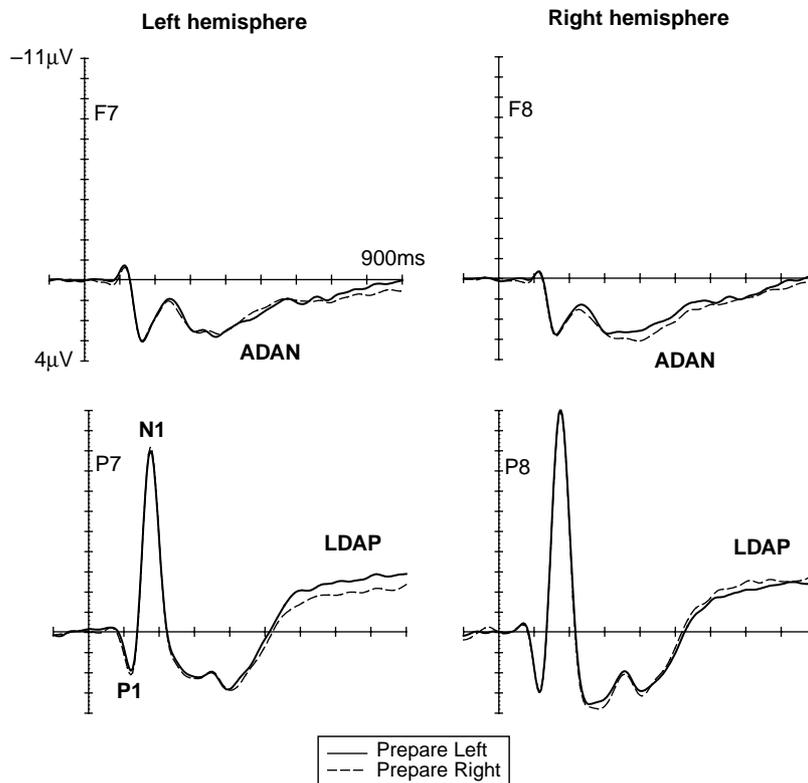


Fig. 1. Grand-averaged ERPs elicited during covert unimanual response preparation over the left and right hemisphere at anterior (F7/8, top) and posterior (P7/8, bottom) electrode pairs. Waveforms show the 900 ms interval following the onset of a visual response cue signalling an upcoming left-hand response (solid lines) or right-hand response (dashed lines), and are collapsed across trials including visual and auditory probes on the left and right side. ADAN, Anterior Directing Attention Negativity; LDAP, Late Directing Attention Positivity.

and was followed by an enhanced posterior positivity contralateral to the side of the anticipated response (LDAP).

The difference waves in Fig. 2 are included to further illustrate the amplitudes and time course of these lateralised ERP modulations elicited during covert response preparation. These waveforms were generated by subtracting ERPs recorded during the preparation of a right-hand response from ERPs elicited during left-hand response preparation, and then subtracting the resulting difference waves for right-hemisphere electrodes from the difference waves for homologous electrodes over the left hemisphere. In the resulting double subtraction waveforms, a negativity contralateral to the side of a cued response is reflected by positive amplitude values (downward-going deflections), and a contralateral positivity is indicated by negative values (upward-going deflections). Fig. 2 shows difference waveforms obtained for anterior (top), central (middle), and posterior (bottom) electrode pairs. An early anterior contralateral negativity (ADAN) started about 350 after cue onset, and was followed by a contralateral positivity at posterior electrodes (LDAP) at about 500 ms. In addition, an enhanced contralateral negativity (LRP) emerged during the later phase of the response preparation interval at C3/4.

These observations were confirmed by statistical analyses. No significant ERP lateralisations sensitive to the side

of a cued response were present in the first 350 ms after cue onset. In the 350–600 ms interval, a significant hemisphere  $\times$  cued response interaction was present at lateral anterior electrodes ( $F(1,15) = 22.2$ ;  $P < .001$ ), reflecting the ADAN component as shown in Figs. 1 and 2. At lateral central electrodes, an electrode site  $\times$  hemisphere  $\times$  cued response interaction was observed ( $F(2,30) = 4.2$ ;  $P < .04$ ;  $\epsilon = .804$ ) and subsequent analyses revealed a significant hemisphere  $\times$  cued response interaction at C3/4 only ( $F(1,15) = 9.0$ ;  $P < .01$ ). At lateral posterior electrodes, the hemisphere  $\times$  cued response interaction approached significance ( $F(1,15) = 4.0$ ;  $P < .07$ ), presumably due to the emergence of the posterior LDAP in the later part of this measurement interval (see Fig. 2)<sup>2</sup>. As can be seen from Fig. 1, the ADAN was more pronounced over the right hemisphere, and post-hoc analyses conducted separately for left and right anterior electrodes confirmed the presence of a significant ADAN over the right hemisphere ( $F(1,15) = 5.7$ ;

<sup>2</sup> This was substantiated by additional analyses conducted for mean amplitudes obtained at lateral posterior electrode pairs between 350 and 475 ms, and between 475 and 600 ms after cue onset, respectively. While there was no indication of any hemisphere  $\times$  cued response interaction in the earlier time window,  $F < 1$ , this interaction was significant in the later time window ( $F(1,15) = 9.1$ ;  $P < .01$ ), reflecting the emergence of the posterior LDAP.

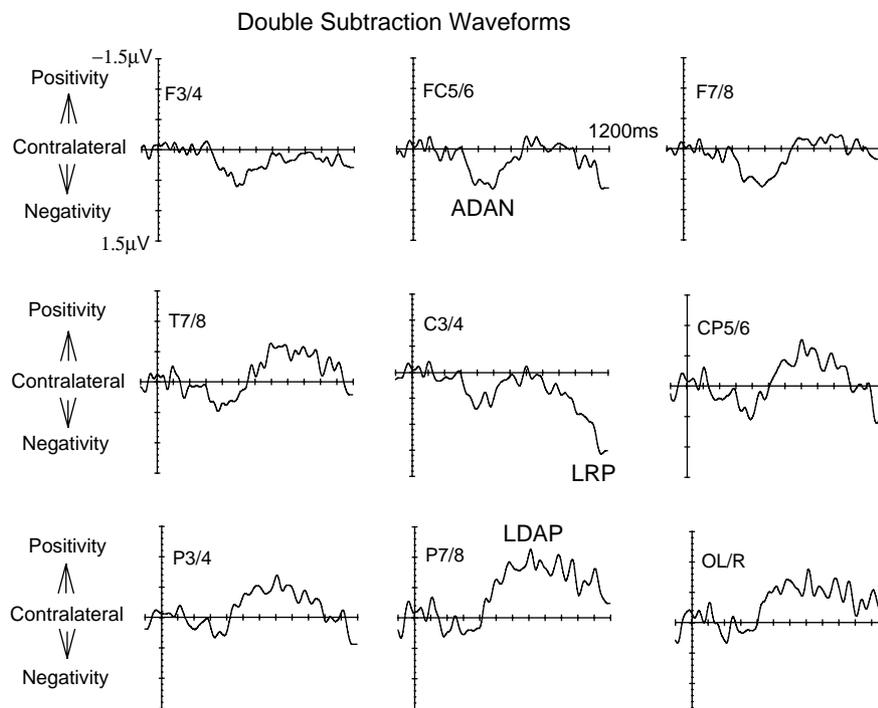


Fig. 2. Difference waveforms obtained at anterior (top), central (middle) and posterior (bottom) lateral electrode pairs during covert unimanual response preparation. Enhanced negativities contralateral to the side of a cued response are reflected by positive values (downward deflections), and enhanced contralateral positivities are reflected by negative values (upward deflections). Three lateralised components (ADAN, LDAP, LRP) were elicited successively and at different recording sites during the response preparation interval.

$P < .04$ ), but no significant differences at corresponding electrodes over the left hemisphere. In the 600–900 ms interval, a hemisphere  $\times$  cued response interaction was obtained at lateral posterior sites ( $F(1,15) = 15.9$ ;  $P < .001$ ), due to the presence of the LDAP component (see Figs. 1 and 2). Follow-up analyses conducted separately for left and right posterior electrodes revealed a significant LDAP over the left hemisphere ( $F(1,15) = 10.8$ ;  $P < .005$ ), and an almost significant effect over corresponding electrodes on the right side ( $F(1,15) = 3.9$ ;  $P < .07$ ). No hemisphere  $\times$  cued response interactions were observed for lateral anterior or central electrodes during this interval. Finally, for the 900–1200 ms interval, no overall hemisphere  $\times$  cued response interactions were found at lateral anterior, central, or posterior sites. However, significant three-way interactions were present at lateral central electrodes and at lateral posterior sites (electrode site  $\times$  hemisphere  $\times$  cued direction:  $F(2,30) = 17.9$  and  $7.5$ ;  $P < .001$  and  $.005$ ;  $\epsilon = .979$  and  $.818$ , respectively). A hemisphere  $\times$  cued direction interaction was observed at C3/4 ( $F(1,15) = 8.6$ ;  $P < .01$ ) in line with the hypothesis that this late contralateral negativity reflects the LRP (see Fig. 2). In addition, a hemisphere  $\times$  cued direction interaction was significant at P7/8 ( $F(1,15) = 7.7$ ;  $P < .02$ ), and approached significance at OL/R ( $F(1,15) = 3.9$ ;  $P < .07$ ), indicating that the posterior LDAP remained present, albeit in attenuated fashion, during the later phase of the response preparation interval.

### 3.3. ERPs elicited in response to visual and auditory probe stimuli

Fig. 3 shows visual ERPs triggered by task-irrelevant visual probe stimuli when these were presented close to the cued hand (solid lines) or close to the uncued hand (dashed lines). Fig. 4 shows ERPs elicited by auditory probes close to the cued versus uncued hand. While unimanual response preparation appeared to have a strong effect on visual ERPs, with enhanced N1 components when visual probes were presented close to the cued response hand, it had little impact on auditory ERPs.

These observations were confirmed by statistical analyses. While response preparation had no significant effects on visual P1 amplitudes, it strongly modulated ERPs to visual probe stimuli in the N1 time range (160–200 ms post-stimulus). Main effects of response preparation were present at lateral posterior and lateral central electrodes as well as at midline sites (all  $F(1,15) > 8.6$ ; all  $P < .01$ ), and this effect was almost significant at lateral anterior electrodes ( $F(1,15) = 4.4$ ;  $P < .06$ ). As can be seen in Fig. 3, N1 amplitudes were enhanced in response to visual probes close to the cued response hand, relative to probes delivered adjacent to the opposite uncued hand. Response preparation  $\times$  electrode site interactions were present at lateral posterior electrodes ( $F(2,30) = 5.2$ ;  $P < .03$ ;  $\epsilon = .644$ ), at lateral central electrodes ( $F(2,30) = 6.1$ ;  $P < .02$ ;  $\epsilon = .616$ ) and at lateral anterior electrodes ( $F(2,30) = 8.9$ ;  $P < .01$ ;

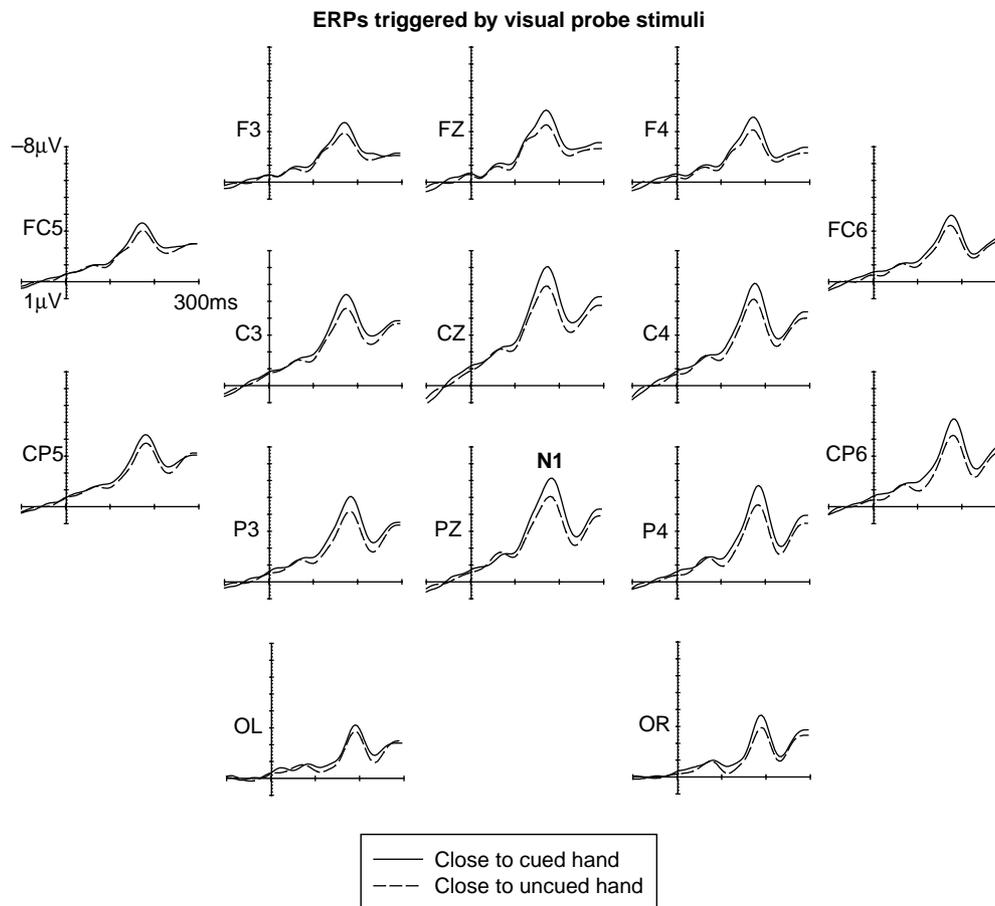


Fig. 3. Grand-averaged visual ERPs elicited by visual probe stimuli delivered 900 ms after response cue onset, relative to a 100 ms pre-stimulus baseline. Solid lines show ERPs triggered by visual probes presented close to the cued hand, and dashed lines show ERPs elicited by probes presented close to the uncued hand.

$\varepsilon = .704$ ). However, follow-up analyses revealed that significant enhancements of N1 amplitudes for visual stimuli close to the cued versus uncued hand were present at all electrode sites, except for F7/8. In the P2 time range (210–250 ms post-stimulus), a significant effect of response preparation was present at lateral posterior electrodes ( $F(1,15) = 5.0$ ;  $P < .05$ ), and approached significance at lateral central sites ( $F(1,15) = 3.7$ ;  $P < .08$ ). This was due to the fact that ERPs triggered by visual probes close to the cued hand remained more negative than ERPs elicited by probes close to the uncued hand beyond 200 ms post-stimulus (see Fig. 3).

In contrast to these clear effects of covert unimanual response preparation on ERPs triggered by visual probe stimuli, no such differences were present for auditory ERPs. As already suggested by the absence of any obvious ERP modulations in Fig. 4, statistical analyses failed to provide any indication for effects of response preparation on auditory ERPs in the N1 and P2 time windows (100–130 ms and 180–220 ms post-stimulus, respectively) at any electrode site investigated, thus suggesting that the processing of auditory probes remained unaffected by

whether these probes were presented close to the cued hand or close to the uncued hand.

#### 4. Discussion

The present experiment investigated whether covert unimanual response preparation would induce lateralised ERP components previously found during cued shifts of spatial attention, and whether it results in spatially selective attentional modulations of visual and auditory stimulus processing. The ERP results obtained in response to visual response cues instructing participants to prepare a left-hand or right-hand response confirmed the findings obtained in our previous study (Eimer et al., 2005) where analogous response cueing procedures were used. An enhanced negativity at anterior electrodes contralateral to the side of the cued response started at about 350 ms post-stimulus. This was followed by an enhanced positivity over contralateral posterior electrodes, as well as by a late contralateral negativity (LRP), which was narrowly focused over lateral central electrodes C3/4. The first two of these

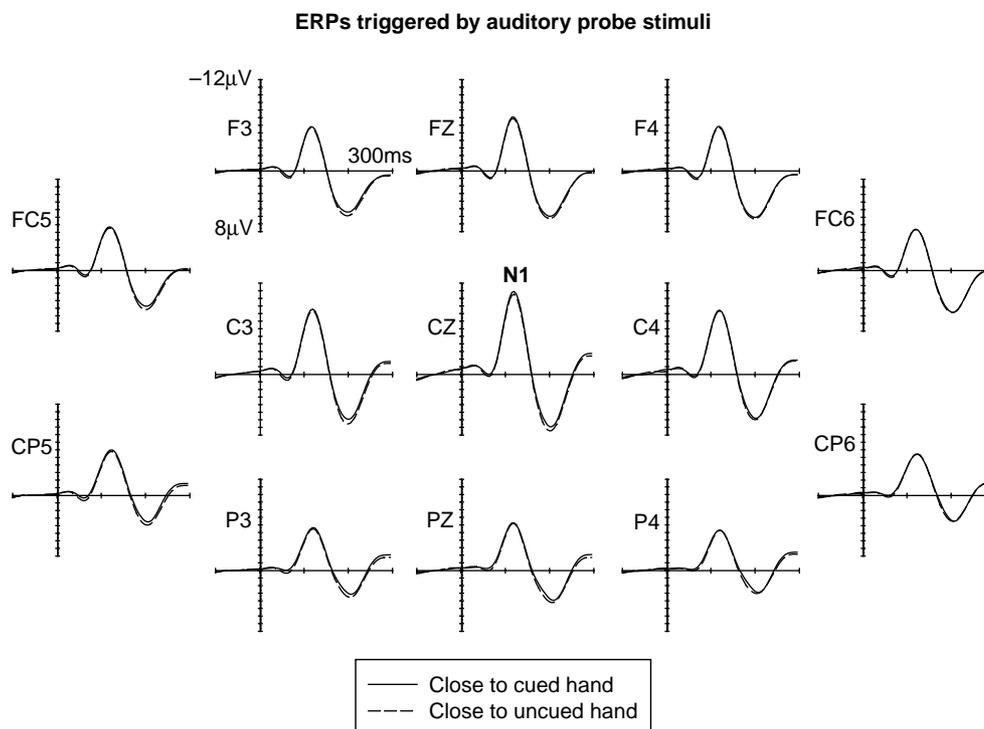


Fig. 4. Grand-averaged auditory ERPs elicited by auditory probe stimuli delivered 900 ms after response cue onset, relative to a 100 ms pre-stimulus baseline. Solid lines show ERPs triggered by auditory probes presented close to the cued hand, and dashed lines show ERPs elicited by probes presented close to the uncued hand.

lateralised components were very similar to the ADAN and LDAP effects observed in earlier experiments where attentional cues explicitly signalled the direction of a covert endogenous attentional shift (Eimer et al., 2002; c.f. Nobre et al., 2000). These two components have previously been interpreted as electrophysiological correlates of covert attentional shifts activated in anticipation of expected task-relevant events at specific locations. The present results confirm that similar ADAN and LDAP components are also elicited when participants prepare a response with their left versus right hand<sup>3</sup>.

The presence of ADAN and LDAP components to response cues strongly suggests that attentional orienting processes are triggered during covert manual response preparation and that these orienting processes might be analogous to those elicited during instructed shifts of covert attention. This is in line with the assumption of the premotor theory of attention that response preparation and attentional shifts are closely linked. This theory further assumes that such close links are due to the fact that attentional orienting

and response preparation are implemented by common control structures. It is important to note that although the ERP modulations observed during response preparation in the present experiment (and in our previous study; Eimer et al., 2005) are consistent with both these assumptions, they only provide direct evidence for the former. The possibility remains that although covert manual response preparation and covert attentional orienting co-occur (as suggested by the presence of ADAN and LDAP components during response preparation), they are still based on anatomically and functionally distinct neural control mechanisms. This issue could be addressed in future experiments, where the direction of covert attention shifts and the direction of covert response preparation are manipulated orthogonally.

The observation that the ADAN was primarily elicited over the right hemisphere in the present experiment is consistent with previous observations from ERP studies that have investigated covert endogenous shifts of visual attention (e.g. Eimer and Van Velzen, 2002; Hopf and Mangun, 2000; Nobre et al., 2000), as well as shifts of auditory attention (Eimer and Van Velzen, 2002). Such a right-hemisphere dominance of brain processes assumed to be involved in attentional orienting has also been observed in functional imaging studies (e.g. Nobre et al., 1997), and points to a specific role of the right hemisphere in the control of spatial attention.

<sup>3</sup> The late contralateral negativity at C3/4 reflects the emergence of the LRP triggered during later stages of the response preparation interval, thereby indicating that the cued response was already partially activated prior to the onset of the imperative visual Go/Nogo stimulus. In previous response precueing experiments where the relevant response hand was specified in advance (c.f. Gratton et al., 1990; Gehring et al., 1992), the LRP was also found to start about 300–400 ms prior to target onset.

The main new question addressed by the present study was whether shifts of attention triggered during covert manual response preparation would result in modulations of visual and auditory processing. If these attention shifts were mediated by modality-unspecific attentional-motor control mechanisms, they should produce spatially selective modulations of probe stimulus processing regardless of the sensory modality of these probes. In other words, manual response preparation should result in systematic effects on visual as well as auditory probe ERP components. To investigate this, visual and auditory ERPs triggered by task-irrelevant visual and auditory probe stimuli presented during the response preparation interval (900 ms after response cue onset) were compared as a function of whether these probes were presented close to the cued hand, or close to the opposite uncued hand. For visual probe stimuli, clear-cut effects of covert response preparation were found (see Fig. 3): Larger visual N1 components were observed when visual probes were presented close to the hand that was currently prepared for an anticipated motor response, as compared to visual probes delivered adjacent to the uncued hand. This effect of unimanual response preparation on visual ERPs was very similar to the effects observed in previous experiments studying crossmodal links in spatial attention (e.g. Eimer and Driver, 2000; Hillyard et al., 1984), where enhanced N1 components were elicited when task-irrelevant visual events were presented at locations relevant for an auditory or tactile task. The fact that visual N1 components were larger when visual probes were presented close to the hand involved in an anticipated response, as compared to probes presented close to the uncued hand, provides clear evidence that visual information processing is also selectively modulated as a result of covert manual response preparation, as predicted by the premotor theory of attention.

In marked contrast to the results obtained for visual probe stimuli, no systematic effects of response preparation were obtained for auditory probes. ERPs triggered by auditory stimuli did not differ as a function of whether these stimuli were presented close to the cued hand or close to the opposite uncued hand (see Fig. 4), thus suggesting that in contrast to visual probes, the processing of auditory events on the left and right side remained unaffected by covert response hand preparation. This finding is clearly at odds with the hypothesis derived from the premotor theory that attentional-motor control circuits activated during covert response preparation are modality-unspecific, and thus induce spatially specific modulations of sensory processing for visual and well as for auditory stimuli.

There are a number of possible reasons why response preparation effects were absent for auditory probes. One could argue that the high intensity of auditory probes (80 dB) resulted in a ceiling effect for auditory ERPs, thus giving little room for cued response preparation to further enhance auditory components. We tested this possibility in a small follow-up study where auditory ERPs were recorded

from 6 participants. Conditions were identical to the present study, except that auditory probe intensity was reduced by 20 dB. In spite of this reduction in loudness, no spatially-specific response preparation effect on auditory ERPs were found for any participant, thus making an explanation in terms of intensity ceiling effects unlikely.

It is also possible that differences in the task-relevance of visual and auditory information may have been responsible for the absence of spatially specific effects of response preparation for auditory ERPs. Whereas auditory events were irrelevant throughout, participants had to process visual response cues and visual imperative stimuli that were presented at fixation. Had audition been made task-relevant (e.g. by using auditory rather than visual cues to indicate response side), systematic response preparation effects might have also been present for auditory ERPs. Although this possibility needs to be investigated in future experiments, it should be noted that previous ERP studies of crossmodal attention have found unequivocal evidence for spatially specific modulations of auditory processing under conditions where auditory stimuli could be entirely ignored (e.g. Eimer and Schröger, 1998; Eimer et al., 2002). These findings suggest that the current results are not primarily determined by the task-relevance of vision and audition.

One could also argue that the absence of spatially specific ERP modulations for auditory probes reflects the relatively poor spatial resolution of audition. Given the superior spatial acuity of vision, visual probes are readily localized as being close to the left or right hand, while the perceived location of auditory probes may be much less distinct. If manual response preparation resulted in a focus of attention that was narrowly focused around the cued response hand, attentional ERP modulations might only be observed for sensory modalities with high spatial resolution such as touch (as in our previous study; Eimer et al., 2005), or vision (the present experiment), but not for audition where spatial localization is less precise. Although consistent with the present findings, an explanation in terms of poor auditory spatial acuity cannot easily account for the fact that experiments investigating crossmodal links in spatial attention (e.g. Eimer and Schröger, 1998; Eimer et al., 2002; Hillyard et al., 1984; Teder-Sälejärvi et al., 1999) have consistently found enhanced auditory N1 amplitudes for tones presented at locations relevant for a visual or tactile task.

Alternatively, it is possible that auditory (but not visual) probes captured attention automatically, regardless of whether they were presented on the cued or uncued side. Irrelevant auditory events have been shown to attract attention involuntarily, thereby affecting the detection and discrimination of subsequent visual targets (McDonald et al., 2000). If auditory probes had captured attention irrespective of their location, no spatially specific effects of response preparation on auditory ERPs should be present, as was indeed the case in the present experiment. However, the

observation that reaction times to visual Go stimuli were significantly faster on trials with auditory probes than on trials with visual probes appears inconsistent with this account. Any capture of attention by peripheral auditory probes should have interfered with the attentional selection of a subsequently presented Go stimulus, and thus should have delayed responses on trials with auditory probes. The fact that RTs were in fact faster on these trials suggests instead that auditory probes interfered less than visual probes with the processing of central visual Go/Nogo stimuli.

There might also be a more general reason as to why vision and touch are systematically modulated by covert manual response activation, whereas auditory processing appears to remain unaffected. This asymmetry might reflect the fact that visual and somatosensory information are generally much more relevant than auditory information for the on-line control of manual response parameters. Accordingly, the activation of specialised attentional-motor mechanisms involved in the control of manual responses might produce spatially selective effects on visual and somatosensory, but not auditory processing. It is important to underline that such an account would imply that such control mechanisms are not fully supramodal, but show a large degree of modality-specificity, reflecting the fact that sensory modalities differ in their relevance for specific types of motor control. Such general differences between modalities might have been emphasized in the present study by the fact that visual stimuli were task-relevant, as they served as response cues and as Go/Nogo stimuli. It would therefore be interesting to investigate whether response preparation would still leave auditory processing unaffected under experimental conditions where auditory stimuli are task relevant. It would also be important to study whether a different pattern of spatially specific sensory modulations can be observed during saccade preparation. Given the fact that eye movements are readily triggered by peripheral sounds, one would expect to find systematic effects of eye movement preparation on auditory ERPs to tones presented during the preparation interval (see also Rorden and Driver, 1999, for initial behavioral evidence for such effects).

In summary, the presence of lateralised ADAN and LDAP components during manual response preparation support the claim of the premotor theory of attention that covert unimanual response preparation is closely linked to spatial attention shifts. However, the additional assumption that such attentional shifts are modality-unspecific has not been confirmed by the present data, as spatially specific modulations were confined to the visual modality, but were entirely absent in audition. Future studies will need to determine whether different results are obtained as a function of changes in task characteristics, or the involvement of other response modalities, such as the oculomotor system.

## Acknowledgements

This research was supported by a grant from the Wellcome Trust. M.E. holds a Royal Society-Wellcome Research Merit Award.

## References

- Butter CM, Bachtel HA, Santucci R. Spatial attentional shifts: further evidence for the role of polysensory mechanisms using visual and tactile stimuli. *Neuropsychologia* 1989;27:1231–40.
- Corbetta M, Akbudak E, Conturo TE, Snyder AZ, Ollinger JM, Drury HA, Linenweber MR, Petersen SE, Raichle ME, Van Essen DC, Shulman GL. A common network of functional areas for attention and eye movements. *Neuron* 1998;21:761–73.
- Deubel H, Schneider WX. Saccade target selection and object recognition: evidence for a common attentional mechanism. *Vision Res* 1996;36:1827–37.
- Driver J, Spence C. Attention and the crossmodal construction of space. *Trends Cogn Sci* 1998;2:254–62.
- Eimer M. The lateralized readiness potential as an on-line measure of selective response activation. *Behav Res Methods Instrum Comput* 1998;30:146–56.
- Eimer M, Coles MGH. The lateralized readiness potential. In: Jahanshahi M, Hallett M, editors. *The Bereitschaftspotential: in honour of professors Deecke and Kornhuber*. Boston, MA/New York: Kluwer /Plenum; 2003. p. 229–48.
- Eimer M, Driver J. An event-related brain potential study of cross-modal links in spatial attention between vision and touch. *Psychophysiology* 2000;37:697–705.
- Eimer M, Driver J. Crossmodal links in endogenous and exogenous spatial attention: evidence from event-related brain potential studies. *Neurosci Biobehav Rev* 2001;25:497–511.
- Eimer M, Forster B. The spatial distribution of attentional selectivity in touch: evidence from somatosensory ERP components. *Clin Neurophysiol* 2003a;114:1298–306.
- Eimer M, Forster B. Modulations of early somatosensory ERP components by transient and sustained spatial attention. *Exp Brain Res* 2003b;151:24–31.
- Eimer M, Schröger E. ERP effects of intermodal attention and cross-modal links in spatial attention. *Psychophysiology* 1998;35:313–27.
- Eimer M, Van Velzen J. Crossmodal links in spatial attention are mediated by supramodal control processes: evidence from event-related brain potentials. *Psychophysiology* 2002;39:437–49.
- Eimer M, Van Velzen J, Driver J. Crossmodal interactions between audition, touch and vision in endogenous spatial attention: ERP evidence on preparatory states and sensory modulations. *J Cogn Neurosci* 2002;14:254–71.
- Eimer M, Van Velzen J, Forster B, Driver J. Shifts of attention in light and in darkness: an ERP study of supramodal attentional control and crossmodal links in spatial attention. *Cogn Brain Res* 2003;15:308–23.
- Eimer M, Forster B, Van Velzen J, Prabhu G. Covert manual response preparation triggers attentional shifts: ERP evidence for the premotor theory of attention. *Neuropsychologia* 2005;43:957–66.
- Farah MJ, Wong AB, Monheit MA, Morrow LA. Parietal lobe mechanisms of spatial attention: modality-specific or supramodal? *Neuropsychologia* 1989;27:461–70.
- Gehring WJ, Gratton G, Coles MGH, Donchin E. Probability effects on stimulus evaluation and response processes. *J Exp Psychol Hum Percept Perform* 1992;18:198–216.
- Gratton G, Bosco CM, Kramer AF, Coles MGH, Wickens CD, Donchin E. Event-related brain potentials as indices of information extraction and response priming. *Electroencephalogr Clin Neurophysiol* 1990;75:419–32.

- Harter MR, Miller SL, Price NJ, LaLonde ME, Keyes AL. Neural processes involved in directing attention. *J Cogn Neurosci* 1989;1:223–37.
- Hillyard SA, Simpson GV, Woods DL, Van Voorhis S, Münte TF. Event-related brain potentials and selective attention to different modalities. In: Reinoso-Suarez F, Ajmone-Marsan C, editors. *Cortical integration*. New York: Raven Press; 1984. p. 395–414.
- Hoffman JE, Subramaniam B. The role of visual attention in saccadic eye movements. *Percept Psychophys* 1995;57:787–95.
- Hopf JM, Mangun GR. Shifting visual attention in space: an electrophysiological analysis using high spatial resolution mapping. *Clin Neurophysiol* 2000;111:1241–57.
- Irwin DE, Gordon RD. Eye movements, attention, and transsaccadic memory. *Vis Cogn* 1998;5:127–55.
- Kustov AA, Robinson DL. Shared neural control of attentional shifts and eye movements. *Nature* 1996;384:74–7.
- McDonald JJ, Teder-Sälejärvi WA, Hillyard SA. Involuntary orienting to sound improves visual perception. *Nature* 2000;407:906–8.
- Michie PT, Bearpark HM, Crawford JM, Glue LCT. The effects of spatial selective attention on the somatosensory event-related potential. *Psychophysiology* 1987;24:449–63.
- Nobre AC, Sebestyen GN, Gitelman GR, Mesulam MM, Frackowiak RSJ, Frith CD. Functional localization of the system for visuospatial attention using positron emission tomography. *Brain* 1997;120:515–33.
- Nobre AC, Sebestyen GN, Miniussi C. The dynamics of shifting visuospatial attention revealed by event-related brain potentials. *Neuropsychologia* 2000;38:964–74.
- Rizzolatti G, Riggio L, Sheliga B. Space and selective attention. In: Umiltà C, Moscovitch M, editors. *Attention and performance*, vol. XV. Cambridge, MA: MIT Press; 1994. p. 231–65.
- Rorden C, Driver J. Does auditory attention shift in the direction of an upcoming saccade? *Neuropsychologia* 1999;37:357–77.
- Rorden C, Greene K, Sasine GM, Baylis GM. Enhanced tactile performance at the destination of an upcoming saccade. *Curr Biol* 2002;12:1429–34.
- Sheliga BM, Riggio L, Rizzolatti G. Spatial attention and eye movements. *Exp Brain Res* 1995;105:261–75.
- Spence C, Driver J. Audiovisual links in endogenous covert spatial attention. *J Exp Psychol Hum Percept Perform* 1996;22:1005–30.
- Spence C, Pavani F, Driver J. Crossmodal links between vision and touch in covert endogenous spatial attention. *J Exp Psychol Hum Percept Perform* 2000;26:1298–319.
- Teder-Sälejärvi WA, Münte TF, Sperlich FJ, Hillyard SA. Intra-modal and cross-modal spatial attention to auditory and visual stimuli: an event-related brain potential (ERP) study. *Cogn Brain Res* 1999;8:327–43.
- Tipples J. Eye gaze is not unique: automatic orienting in response to uninformative arrows. *Psychon Bull Rev* 2002;9:314–8.
- Van der Lubbe RHJ, Wauschkuhn B, Wascher E, Niehoff T, Kömpf D, Verleger R. Lateralized EEG components with direction information for the preparation of saccades versus finger movements. *Exp Brain Res* 2000;132:163–78.
- Van Velzen J, Eimer M. Early posterior ERP components do not reflect the control of attentional shifts towards expected peripheral events. *Psychophysiology* 2003;40:827–31.
- Van Velzen J, Forster B, Eimer M. Temporal dynamics of lateralized ERP components elicited during endogenous attentional shifts to relevant tactile events. *Psychophysiology* 2002;39:874–8.
- Verleger R, Vollmer C, Wauschkuhn B, van der Lubbe R, Wascher E. Dimensional overlap between arrows as cueing stimuli and responses? Evidence from contra-ipsilateral differences in EEG potentials. *Cogn Brain Res* 2000;10:99–109.
- Ward LM. Supramodal and modality-specific mechanisms for stimulus-driven shifts of auditory and visual attention. *Can J Exp Psychol* 1994;48:242–59.
- Wauschkuhn B, Wascher E, Verleger R. Lateralised cortical activity due to preparation of saccades and finger movements. *Electroencephalogr Clin Neurophysiol* 1997;102:114–24.
- Yamaguchi S, Tsuchiya H, Kobayashi S. Electroencephalographic activity associated with shifts of visuospatial attention. *Brain* 1994;117:553–62.